ARE FLUCTUATIONS INHERITED?[1]

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THE object of this paper is to present certain facts in regard to the inheritance of fluctuations which have been obtained from a study of the common garden pea (*Pisum sativum*). While an experiment was being conducted to study the effect of fertility upon the fluctuating variability of certain characters, data were also obtained to show to what extent these fluctuating characters are inherited. The peas used were a mixed population and not a pure line, and had not been selected for any particular character when the experiment was started.

The belief has long been held that the improvement of animals or plants could be obtained by selecting from the best individuals, or those possessing to the greatest degree the quality desired.

The fact is that at present most of our agricultural breeding and improvement is based upon this belief and this is the method which is most generally followed in practical breeding. This view held sway from the time of the earliest breeders until the appearance of the Mutation Theory by DeVries. It was first stated scientifically by Darwin in his "Origin of Species," for Darwin, after a study of the evidence accumulated, was convinced that the improved breeds had been obtained in this manner. He says:

> We can not suppose that all the breeds were suddenly produced as perfect and as useful as we now see them; indeed, in many cases we know that this has not been their history. The key is man's power of accumulative selection: nature gives successive variations; man adds them up in certain directions useful to him. In this sense he may be said to have made for himself useful breeds.[2]

[1] Contribution VI, Laboratory Experimental Plant-breeding, Cornell University. The writer expects to follow with a series of articles on the same subject.

[2] "Origin of Species," Chapter 1, p. 35, Murray Edition.

He further states:

> If selection consisted merely in separating some very distinct variety, and breeding from it, the principle would be so obvious as hardly to be worth notice; but its importance consists in the great effect produced by the accumulation in one direction, during successive generations, of differences absolutely inappreciable by an uneducated eye—differences which I for one have vainly attempted to appreciate.[3]

DeVries after much careful experimentation and study of results of agricultural breeding (mainly the results at Svalöf and those of the German breeders) showed that much of the improvement which has occurred was not due to cumulative selection but must be explained in some other manner.

In recent years much careful scientific work has been done along this line to test the action of selection within a pure line and in a mixed population.

The Svalöf Experiment Station has done much in practical plant-breeding to show that, with reference to the cereals especially, the effect of selection went no further than to isolate the pure lines, and when this was accomplished no further gain was made by selection.

Johannsen,[4] working with beans and Jennings[5] with *Paramecium*, have arrived at the same general conclusion which has been summed up by Pearl[6] as follows:

> From a mixed "general" population it is possible by a single selection to isolate pure strains ("pure lines," "homozygote strains," "pure races") which will breed true and not revert to the mean of the general population from which they were isolated, regardless of whether further selection is practised or not. It is impossible to demonstrate any cumulative effect of continued selection within the pure strain. Continued breeding from the extreme individuals of such a pure strain ("fluctuating" variants) does not change the mean of that strain. From these considerations it follows that it will be difficult or impossible to make any definite and permanent change in the mean of a general population simply and solely by continued selection of extreme indi-

[3] *Loc. cit.*, p. 36.

[4] "Uber Erblichkeit in Populationen und in reinen Linien," Jena, 1903.

[5] "Heredity, Variation and Evolution in Protozoa, II," Heredity and Variation of Size and Form in *Paramecium* with Studies of Growth, Environmental Action and Selection, *Proc. Amer. Phil. Soc.*, Vol. XVI, pp. 393–546, 1908.

[6] "Is there a Cumulative Effect of Section?" *Abstammungs- und Vererbungslehre,* 2, 1909, H. 4.

viduals, because in the vast majority of cases such individuals will be extreme fluctuating variants rather than mutants.

Jennings[7] states in his paper that "Systematic and continued selection is without effect in a pure race, and in a mixture of races its effect consists in isolating the existing races, not in producing anything new." And concludes[5] that "Until some one can show that selection is effective within pure lines it is only a statement of fact to say that all the experimental evidence we have is against this."

Recently Pearl[6] has brought forth a very noteworthy contribution in this line. His evidence is based upon the work which is being done at the Maine Agricultural Experiment Station to determine the effect of selection on fecundity and the inheritance of fecundity in poultry. His conclusions may be summed up as follows:

> Selection for high egg production carried on for nine consecutive years did not lead to any increase in the average production of the flocks.
>
> The present data give no evidence that there is a sensible correlation between mother and daughter in respect to egg production, or that egg-producing ability (fecundity) is sensibly inherited.
>
> In this experiment the daughters of "200-egg" hens did not exhibit, when kept under the same environmental conditions, such high average egg production as did pullets of the same age which were the daughters of birds whose production was less than 200 eggs per year.

Professor Waugh,[8] of the Massachusetts Agricultural Experiment Station, has been making some studies of the variation of peas and the inheritance of the different fluctuating characters. He has found that the coefficients of heredity for the different characters are very low and are not very significant in the case of any one character. The two characters, length of vine and number of pods per vine, show a coefficient of heredity of .170 and .158, respectively. At the same time he found that there were certain lines that did reproduce their characters to an appreciable extent, which is along the

[7] "Heredity and Variation in Simplest Organisms," AMER. NAT., June, 1909.

[8] Twenty-first Ann. Rept. Mass. Agr. Exp. Sta., Part II.

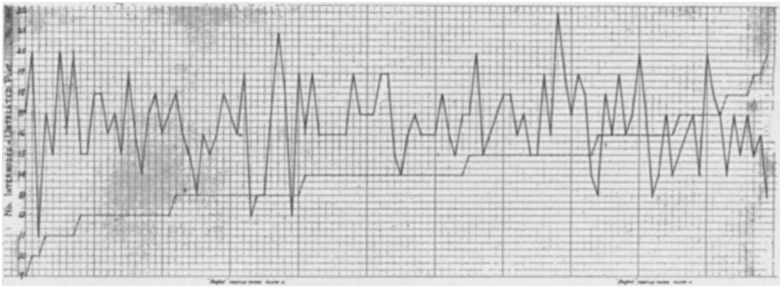

FIG. 1. Diagram showing the relation between parents and offspring in regard to number of internodes on the untreated plot. The broken line represents the parents and the solid line the offspring.

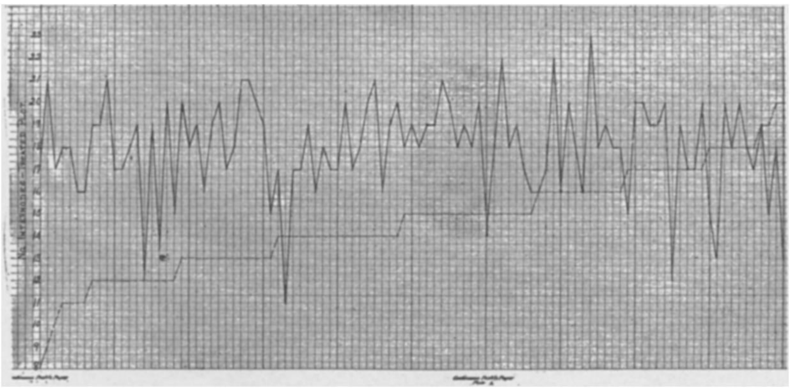

FIG. 2. Diagram showing the relation between parents and offspring in regard to number of internodes on the treated plot. The broken line represents the parents and the solid line the offspring.

line of other studies dealing with pure lines which have been reported.

The evidence which the writer here presents is not based upon large enough numbers to be conclusive in itself, but it is certainly suggestive and adds to the facts already brought together. The number of individuals used is as large as is used many times in the beginning of a practical experiment to develop a strain by selection.

Plan of the Experiment.—The writer studied the variability of peas when grown on plots of different fertility, and in carrying this study on a second generation the planting was done in such a way that the parentage of each plant was known. That is, each plant of the

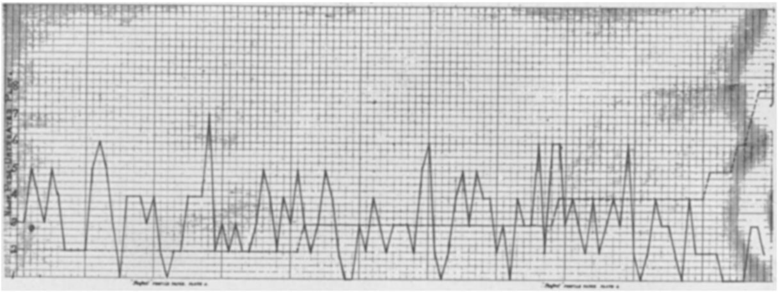

FIG. 3. Diagram showing the relation between parents and offspring in regard to number of pods on the untreated plot. The broken line represents the parents and the solid line the offspring.

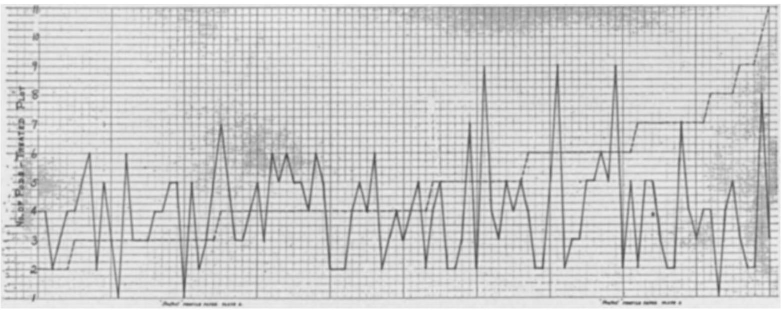

FIG. 4. Diagram showing the relation between parents and offspring in regard to number of pods on the treated plot. The broken line represents the parents and the solid line the offspring.

second generation plants was planted from certain parent plants, and the records were kept in such a way that the characters of the offspring could be compared with those of the parents. As stated above, the number of individuals was of necessity small, yet since the study was made under two different soil environments it seems quite representative of what one is to expect in ordinary selection work.

The difference between this study and regular selection work is that no selection of parents was made, while in ordinary selection work the best individuals are saved for planting.

These data are presented to answer the questions—"What basis have we to expect a cumulative effect of selection? Do we find the resulting offspring following the law of regression?"

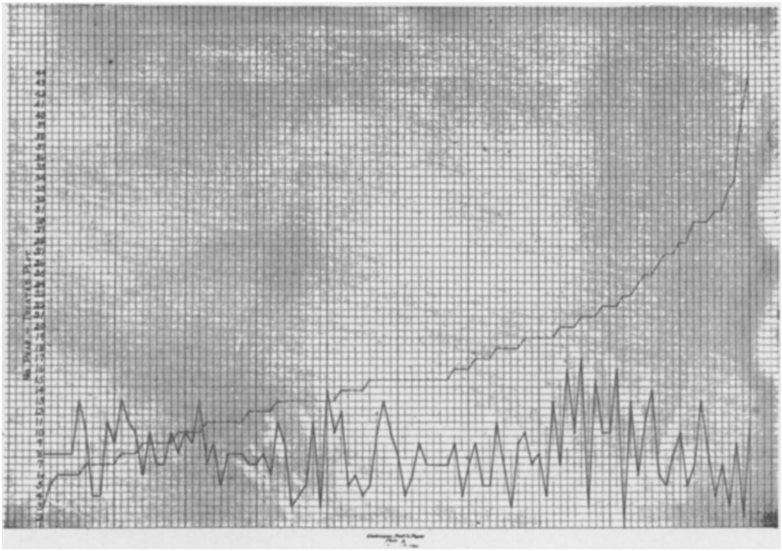

FIG. 5. Diagram showing the relation between parents and offspring in regard to number of peas on the treated plot. The broken line represents the parents and the solid line the offspring.

Regression tables were made for several characters obtained from the plants studied. Such characters as, height of plant, number of internodes, number of pods, number of peas and yield of seed were observed. The results of these calculations are shown in Table I.

TABLE I

Character	Coefficients of Heredity Ordinary Soil Plot	Fertilized Plot
Number of internodes	.027 ± .064	—.050 ± .067
Number pods per plant	—.235 ± .061	.012 ± .067
Number peas per plant	—.152 ± .063	—.045 ± .067
Height of plant	—.191 ± .062	.014 ± .067
Yield of plant (peas in grams)	—.100 ± .064	.001 ± .067

We see that the coefficients of heredity are very low and some of them are even negative. This shows that as far as this data is concerned these fluctuating characters do not follow the law of regression to any appreciable extent. No emphasis should be placed upon the fact that some of these coefficients are negative, but the point is that they are not positive to any noticeable degree. The charts (Figs. 1–9) show in a graphic manner

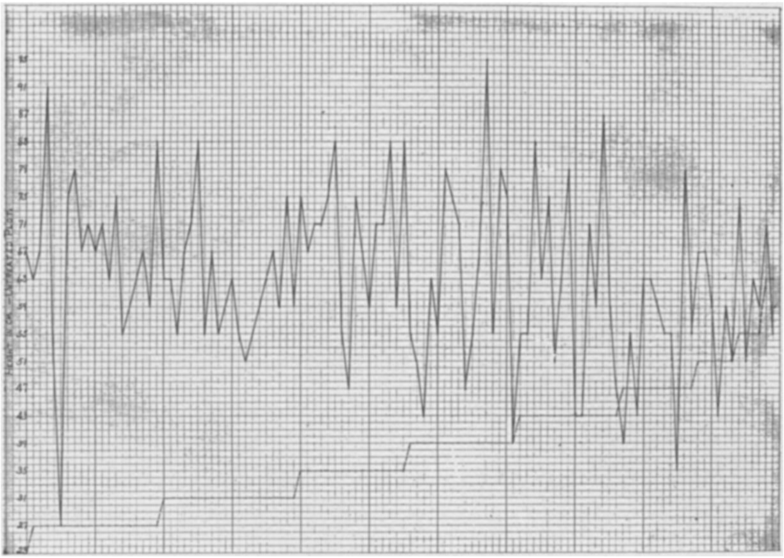

FIG. 6. Diagram showing the relation between parents and offspring in regard to height on the untreated plot. The broken line represents the parents and the solid line the offspring.

the lack of inheritance for these different characters. In each case the dotted line represents the parent plants and the solid line the offspring. These point out some very interesting facts. While we find that in general the coefficients of heredity are practically negligible quantities, yet there are certain parents which reproduce some of their characters. This we are to expect from our knowledge gained by the study of populations. That is, in the study of a mixed population we expect to find certain lines which will reproduce to a marked degree.

The charts show that the line representing the offspring for any certain character seems to rise or fall independently of the value of the parental plant. These diagrams show how in some cases the line for the offspring tends to go down rather than up, but no conclusion must be drawn from this other than that it does not follow the parent line and rise as the parent line does.

Often there arises a question in the minds of those believing in cumulative selection, which may be stated as follows: If we take any population and group it ac-

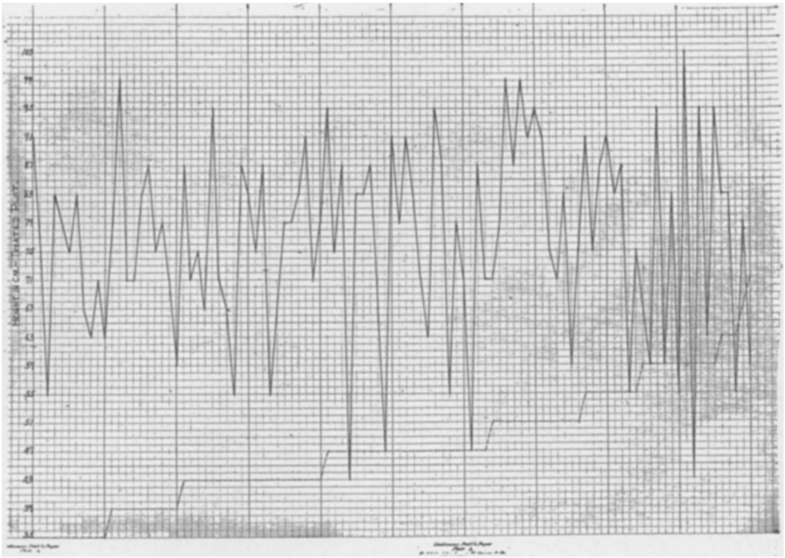

FIG. 7. Diagram showing the relation between parents and offspring in regard to height on the treated plot. The broken line represents the parents and the solid line the offspring.

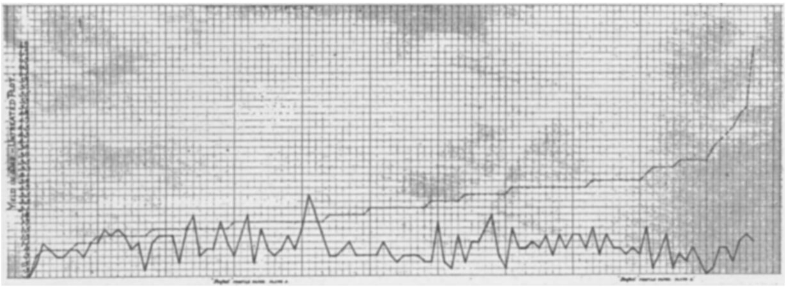

FIG. 8. Diagram showing the relation between parents and offspring in regard to yield on the untreated plot. The broken line represents the parents and the solid line the offspring.

cording to any certain character and select from above or below the mean, will not the progeny resulting from the individuals above the mean possess this character to a greater degree than those coming from parents below the mean?

To answer this the writer has arranged the data in the following manner: The individuals used as parents were divided into two parts, the lower half, or the half possessing the character in question in the least degree,

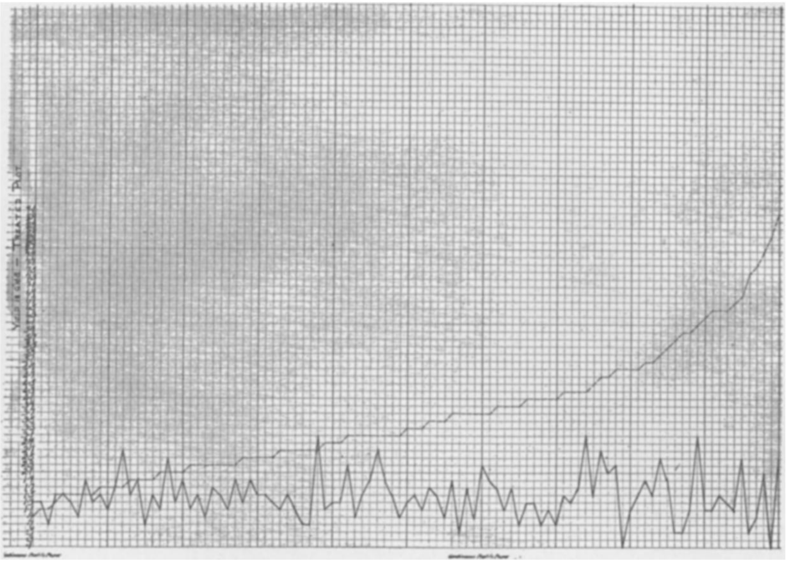

FIG. 9. Diagram showing the relation between parents and offspring in regard to yield on the treated plot. The broken line represents the parents and the solid line the offspring.

and the upper half. The resulting offspring was again averaged for the different characters and the results are shown in Table II.

TABLE II

AVERAGES FOR THE DIFFERENT CHARACTERS

Character,	First Half.		Second Half.	
	Parent.	Offspring.	Parent.	Offspring.
Height, untreated	30.6	65.3	45.0	60.7
" treated	41.2	75.4	53.7	77.7
Internodes, untreated	12.6	16.5	15.8	16.5
" treated	12.8	17.9	16.5	18.0
Number pods, untreated	2.2	3.2	3.9	3.0
" " treated	3.4	3.9	6.3	4.0
Number peas, untreated	6.4	5.9	12.7	4.8
" " treated	10.5	8.3	22.2	8.1
Yield, untreated	1.493	1.048	3.011	.889
" treated	2.260	1.476	4.986	1.453

Again, the individuals were divided into three parts as follows: The first third, or those in which the average of any character for the parents was the lowest, the

second or middle third, or those near the mean, and the third third, or those in which the average for the parents was the highest. The average was obtained for the different characters in the offspring produced from these different lots of parents and the results tabulated and shown in Table III.

TABLE III

AVERAGES FOR THE DIFFERENT CHARACTERS

Character.	First Third.		Second Third.		Third Third.	
	Parent.	Off-spring.	Parent.	Off-spring.	Parent.	Off-spring.
Height, untreated	28.7	64.1	36.8	65.4	48.	59.6
" treated	39.2	75.1	46.6	77.1	56.8	77.5
Internodes, untreated	12.1	16.2	14.1	16.8	16.4	16.4
" treated	12.1	17.7	14.6	18.3	17.2	17.8
Number pods, untreated	2.	3.3	2.9	3.1	4.4	2.8
" " treated	3.1	3.9	4.4	4.1	7.1	4.0
Number peas, untreated	5.6	5.6	8.8	5.8	14.2	4.7
" " treated	8.9	8.5	15.	7.3	25.5	8.8
Yield, untreated	1.311	1.044	2.100	.972	3.343	.889
" treated	1.941	1.453	3.335	1.453	5.688	1.488

We see that there is no general increase for the value of the different characters as we pass from the lower half to the upper half, or from the lower third to the middle or upper third. In some instances there is an increase, in others a decrease. That is, the individuals resulting from the parents above the mean do not possess the character to any greater degree than those resulting from parents below the mean. We see then that these data answer the question in the negative; or to take a concrete case, the number of peas per plant on the untreated plot show that plants resulting from the upper half of the parents *do not produce* any more peas per plant than those coming from the lower half. The results are as follows:

Average of Parents	Average of Offspring
6.4	5.9
12.7	4.8

The two tables show very clearly that as far as this data are concerned, there is no difference in the offspring resulting from high or low averaging parents.

As peas are self-fertilized, it will be of interest to note some results obtained with a cross-fertilized crop. The writer has obtained data from selection experiments in corn which are very interesting in this connection. While selecting for yield and earliness data have been obtained which tend to show that corn is not different from peas and that in general fluctuations are not inherited, but that certain individuals reproduce to a high degree. The results obtained with yield are shown in the following table.

TABLE IV

	Average Yield of Parents	Average Yield of Offspring
Plot 1	46.6 lbs. per row	43.0 lbs. per row
Plot 1	52.5 lbs. per row	44.8 lbs. per row
Plot 2	27.2 lbs. per row	81.5 lbs. per row
Plot 2	34.1 lbs. per row	76.2 lbs. per row

While making these studies the effect of the size of seed planted on the offspring was determined. In planting the second generation plants, unfortunately, the seeds were not weighed, but an average seed from each parent was taken and planted. The chances are that by selecting in this manner an average sized seed would be obtained, and since the average weight seed for each parent plant is known, it seems fair to assume that the seed planted approached the average weight of seed. Regression tables were arranged for the two plots in which the height of plant for the offspring was correlated with the average weight of seed for the parent plants. These tables show that as the average weight of seed planted increases, the height or size of the resulting plant also increases. Although the coefficient is not high in either case, yet it is higher on each of the plots taken than that determined for any character. This seems to show that the size of seed, regardless of the plant from which it came, has more influence on the offspring than the parent plant itself. The coefficient is $.276 \pm .059$ for the untreated plot and $.139 \pm .066$ for the treated plot.

Waldron[9] has shown that large (heavy) seed in oats

[9] "A Suggestion Regarding Heavy and Light Seed Grain," AMER. NAT., Vol. XLIV, January, 1910.

comes from the shorter culms and suggests that in selecting large seed for planting we are selecting from small plants. This may be true. The writer finds that the average weight of seed in peas decreases with the height of plant, which corresponds to the results obtained by Waldron. On the other hand, when these are planted the larger seed, although coming from smaller (shorter) plants, produced larger plants than smaller seed which came from the large plants.

The foregoing results then indicate that there is not enough evidence in favor of the inheritance of fluctuations caused by environment to form a practical working basis. That is, by selecting out the individual plants which give an exceptionally high yield we would not obtain any higher yielding individuals than from a selection taken at random.

We find then that we have given a definite answer to the question which is the title of this paper.

While such statements do not accord with those who place their faith in cumulative selection, yet it is only a statement of fact as shown by an analysis of such data as are here brought together.

These results accord very closely with those stated by Pearl[6] and we can agree with a statement made by him which is as follows:

> Altogether much evidence is accumulating from widely different sources to show that simple selection of superior individuals as breeders can not alone be depended upon to insure definite or continued improvement in a strain. Some improvement may possibly follow this method of breeding at the very start but the limits both in time and amount are very quickly reached.

The rapidly accumulating facts in this respect bring us to face a different view of the value of selection. The testing of individuals to learn their power to reproduce their characters must be done just the same but a different interpretation must be given the results obtained.

Unless further studies produce different results, we can say from the facts at hand that there is no evidence to show that a basis exists for cumulative selection.